The Reproductive Cycle of Interior Spruce

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PREFACE

British Columbia has 25 native conifer species of which 15 are commercially important and scheduled for reforestation. Tree improvement programs for four of these species are now under way and programs for several other species are planned. A necessary prerequisite for extensive reforestation and tree improvement programs is a complete understanding of the reproductive cycle of each species.

Until 1970, Douglas-fir was the only native species for which the complete reproductive cycle was known. Since that time, studies of the reproductive cycles have been completed for 13 of the other commercially important conifers. These studies include descriptions of vegetative bud and shoot development as they relate to cone initiation, the time and method of cone initiation, predormant and postdormant cone-bud development, pollen development, pollination, and embryo and seed development. Although these studies provide essential details of the reproductive cycles, a more general description of all aspects of the reproductive cycle of a particular species is frequently requested.

This request has resulted in a series of short books concerning the reproductive cycles of several conifers. Serving as ready references for foresters and others concerned with seed production and tree improvement, these books will explain the complete reproductive cycle; provide useful guidelines for cone induction studies; assist in forecasting pollen and seed production; enable more effective pollination; and provide some clues to the causes of poor seed production. In addition, such information should be useful to students of forestry and biology at universities, technical schools and high schools.

This book, *The Reproductive Cycle of Interior Spruce*, is not meant to include a complete literature review. Only the most pertinent and accessible references are cited and listed, providing a source for numerous related reports.

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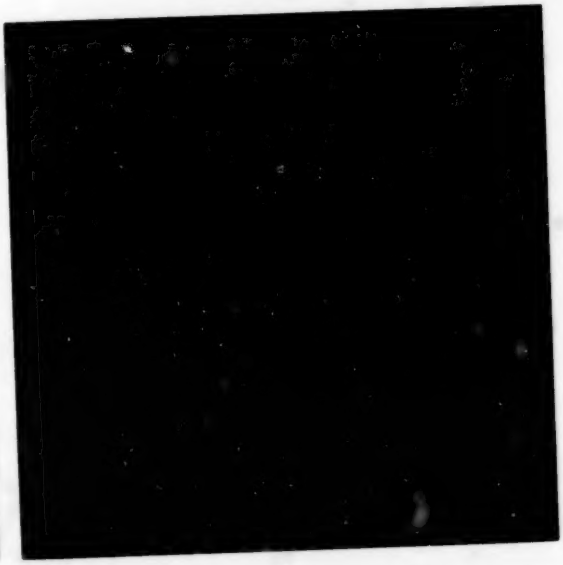
The Reproductive Cycle of Interior Spruce



Introduction

Interior spruce is the name commonly used for both white spruce (*Picea glauca* (Moench) Voss) and Engelmann spruce (*Picea engelmannii* Parry) in the interior of British Columbia.

The spruces, genus *Picea*, are members of the largest family of conifers, the Pinaceae. Some 40 (Safford 1974) to 50 (Ogilvie and Rudloff 1968) species of *Picea* occur in north temperate regions of Europe, Asia and North America. In North America there are six (Rehder 1960; Ogilvie and Rudloff 1968) to nine[1] species in two groups: a more ancient *Picea rubens* - *mariana* group in the northeast; and a *Picea glauca* - *engelmannii* - *pungens* - *sitchensis* group which occurs primarily in the west. The latter group is believed to have originated more recently from an ancestral type that formed a link between Asiatic and North American spruces. It has been suggested that the fossil *P. banksii*, or possibly *P. glauca*, represents this link (Ogilvie and Rudloff 1968).

Placement of the four western species into one group is based on their morphological similarities and their ability to hybridize with one another. Both *P. glauca* and *P. engelmannii* have been suggested to represent a central position in this group (Nienstaedt and Teich 1972). *Picea engelmannii* and *P. pungens* (Colorado blue spruce) are most similar in morphological features. *Picea glauca* and *P. engelmannii* also are similar and it has been suggested that the latter be considered as a subspecies of *P. glauca* (Taylor 1959). Recently, however, chemical comparisons of leaf extracts and leaf oil terpenes have shown that these two species, though quite similar, should be separate (Ogilvie and Rudloff 1968). Consequently, *P. glauca* and *P. engelmannii* will be treated here as separate species which overlap in distribution and may hybridize, forming intermediate individuals sharing traits of both parents. Such hybridization is not unique to these two species but is common between many species of spruce (Neinstaedt and Teich 1972; Daubenmire 1974; Fowler and Roche 1976). For this reason and because the genus is large, heterogeneous, and widely distributed, taxonomy within the genus is complex.

Distribution and Taxonomy

White spruce (Fig. 1) is one of the most widely distributed conifers in North America (Fowells (compiler) 1965; Nienstaedt and Teich 1972). It extends from western Alaska to eastern Newfoundland and from the tundra in the north, southward into Montana, Minnesota, Wisconsin, Michigan, and the New England states. It occurs in most of the

FIGURE 1. White spruce branch and mature, open cones. (X 1)

[1]Gyula Kiss, personal communication, 1982, B.C. Ministry of Forests, Research Branch, Victoria.

northeastern interior of British Columbia, east of the main range of the coastal mountains (Fig. 2). Its range overlaps with Sitka spruce in the same northern coastal regions of British Columbia where hybridization and intermediate forms are evident. White spruce is a low-elevation interior species generally occurring below 1000 m. Above this elevation it intergrades with Engelmann spruce in many locations (Fig. 4).

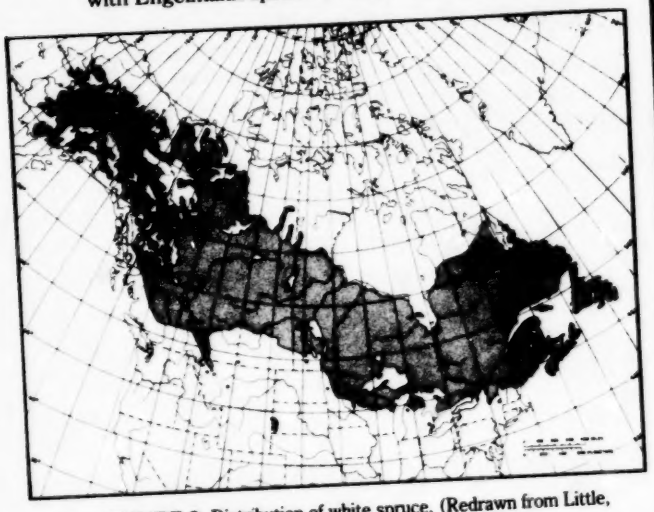


FIGURE 2. Distribution of white spruce, (Redrawn from Little, 1971.)

Englemann spruce (Fig. 3) has a more restricted and scattered distribution than white spruce (Fowells (compiler) 1965; Fowler and Roche 1976). It occurs east of the coastal mountains in British Columbia and extends to just beyond the Alberta border (Fig. 4). It extends southward in the Rocky Mountains to New Mexico and Arizona, and in the Cascade Mountains to Northern California. At the northern limits of its range it may occur as low as 610 m elevation, but it becomes restricted to higher elevations further south, where it may be found at the 3250 m elevation in the central and southern Rocky Mountains. Its range overlaps with white spruce throughout much of the interior of British Columbia where white spruce occupies lower elevations in the same regions. Engelmann spruce occurs in association with Colorado blue spruce in scattered locations throughout much of the central Rocky Mountains. In these areas, hybrids occur which are intermediate in chemical and morphological character (Fowler and Roche 1976).

FIGURE 3. Engelmann spruce branch and mature, closed cones. (X 0.2)

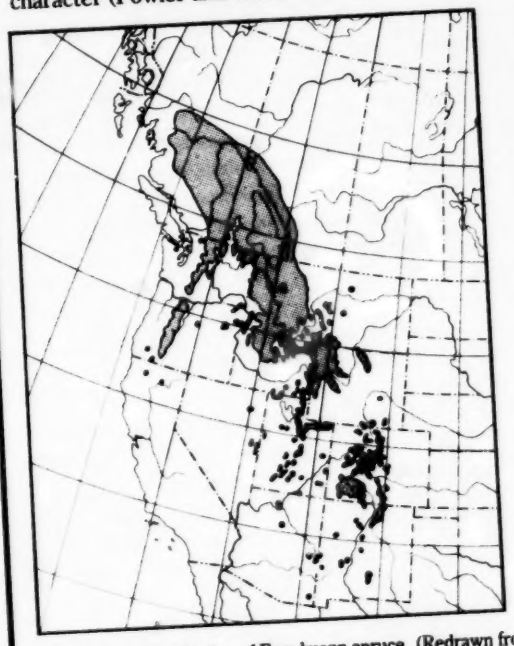


FIGURE 4. Distribution of Engelmann spruce. (Redrawn from Little, 1971.)

Economic Importance

The wide distribution of white spruce, the predominance of the species in many regions, and its value as a source of timber products make it, along with its hybrid forms, the most extensively harvested tree in British Columbia. The greatest use of white spruce is pulpwood, but other uses include lumber of all kinds, veneer and many specialty wood products (Hosie 1975).

Engelmann spruce is economically less valuable than white spruce because the former has a more limited distribution, seldom forms pure stands, is often relatively inaccessible, and is generally slower growing. Where it is harvested with white spruce it is not distinguished from the latter and is used for the same timber products. Engelmann spruce is particularly important in the ecology of high-elevation areas: as protective cover for watersheds; as wildlife habitat; for recreation; and as a major component in the long-term maintenance of the alpine environment.

Reproductive Potential

White spruce at lower elevations is a relatively good cone producer. Cones rarely appear on trees as young as 10 years old, and cones in any quantity usually do not occur until trees are over 30 years old. Heavy cone crops occur at lower elevations every 5 to 10 years, with occasional light crops in intervening years. At higher elevations, heavy cone crops are generally less frequent. Mature trees bear abundant cones in the upper region of the crown and each cone potentially may produce as many as 150 to 200 seeds. However, only about 30 filled seeds are usually produced per cone (Nienstaedt and Teich 1972).[1]

Engelmann spruce, perhaps because it is a higher-elevation species, normally does not begin to produce cones until trees are 16 to 25 years old. Good cone crops may occur every 2 to 5 years, with light crops in intervening years (Fowler and Roche 1976). In good cone-crop years, Engelmann spruce produces abundant cones, but generally it is less prolific than white spruce, primarily because it characteristically inhabits a cold, humid habitat which is not conducive to cone-bud initiation. Potential seed yield is about 200 seeds per cone but because of the many problems encountered in seed development at higher elevations, the number of filled seed is generally lower than in white spruce. Added to these problems of seed and cone production is the difficulty often encountered in harvesting cones from higher elevations.

The wide distribution, utility, and economic importance of the two species make them valuable for reforestation. Extensive reforestation requires a constant supply of high quality, yet economical seed. In response to this need, genetic tree improvement programs in British Columbia have begun for both species. Seed orchards have been established in the interior and are planned for coastal-interior transition regions of the province. Their management for maximum production of filled seed will require a thorough understanding of each species' complete reproductive cycle. This must include the important events during the 15 months from the time of cone initiation in the summer and pollination of these cones the following spring, through fertilization and embryo development in the summer until seed is mature and shed in the fall of the year the cones were pollinated (Fig. 5).

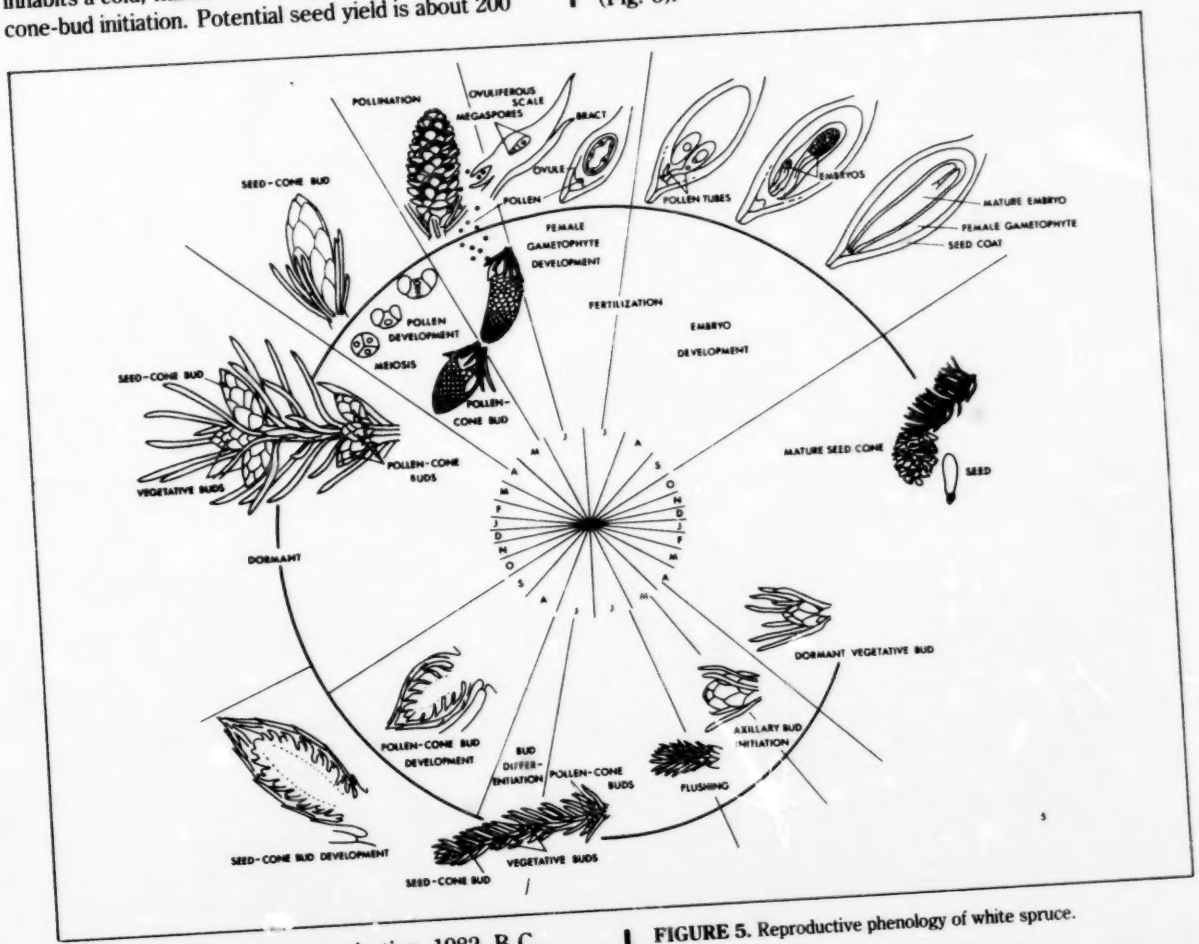


FIGURE 5. Reproductive phenology of white spruce.

[1]Gyula Kiss, personal communication, 1982, B.C. Ministry of Forests, Research Branch, Victoria.

Reproductive Phenology

The reproductive cycles of white and Engelmann spruce are essentially the same in anatomical detail. The main difference is in the phenology, or chronology, of reproductive development. Although the phenology of the two species is similar at intermediate elevations, it is quite different when low-elevation white spruce is compared with moderate or high-elevation Engelmann spruce. Within either species, the occurrence of a particular event may vary by more than one month between individuals at the extremes of their distribution. Phenological differences between the two species in extremes of their distribution will vary even more. Consequently, the phenology given here is that of white spruce growing at lower elevations in central British Columbia (Fig. 5). This will be compared with the phenology of Engelmann spruce at higher elevations in the same region.

Although the phenology will vary with elevation and geographical distribution, the sequence and details of reproductive development remain the same, and a single general description of the reproductive cycle is valid (Fig. 5).

Vegetative Bud and Shoot Development

Vegetative bud and shoot development are similar in white and Engelmann spruce, but the phenology varies with latitude and elevation (Owens *et al.* 1977; Harrison and Owens 1982). Trees in northern or high-elevation regions may begin development later in the spring and stop development earlier in the fall than trees in southern or low-elevation regions. However, developmental events during the summer or middle of the growth cycle occur at about the same time in both species in most regions. A typical example of low-elevation white spruce is shown in Figure 6. Because cone buds are initiated on the elongating shoot, which develops from the vegetative bud, it is important to understand vegetative bud and shoot development.

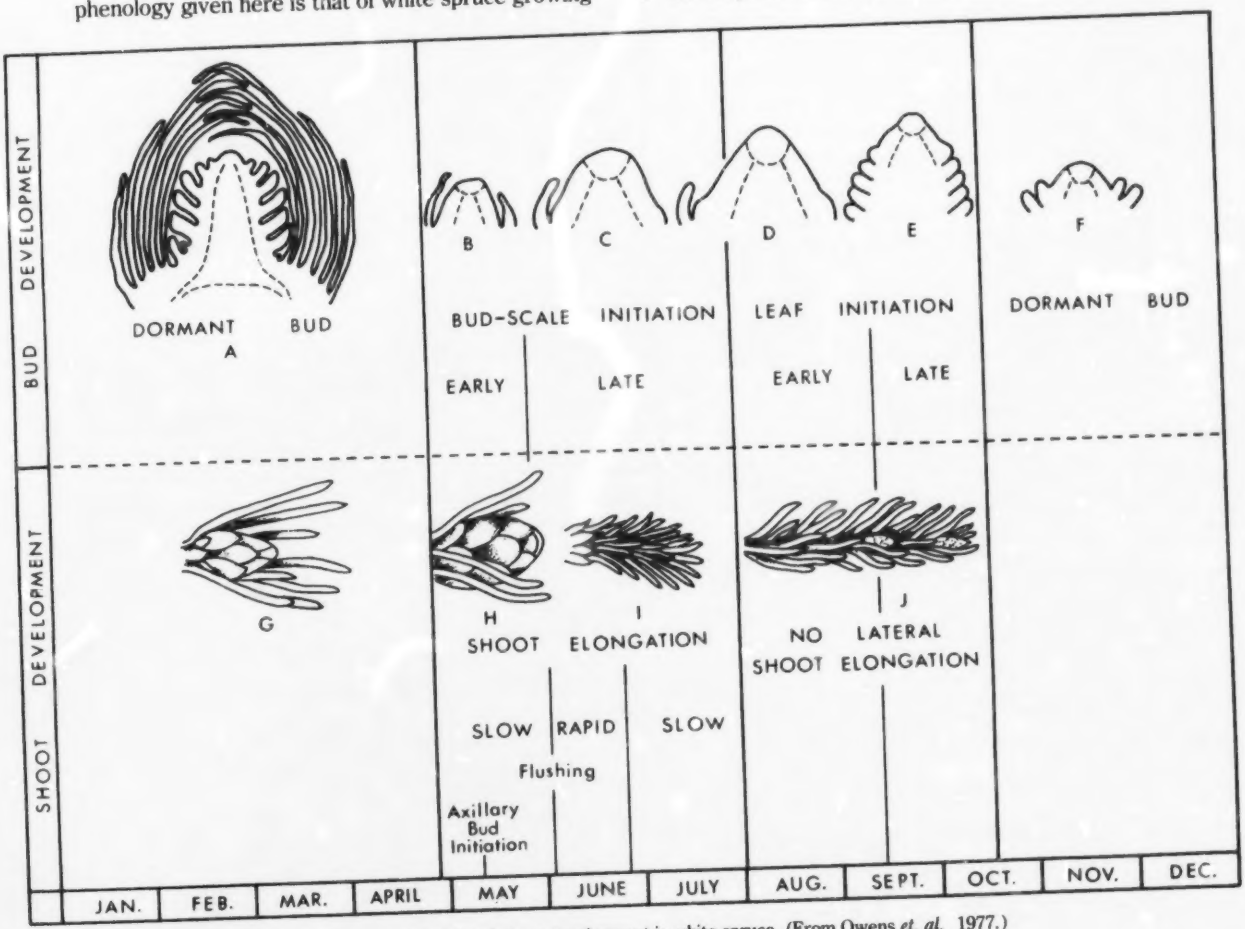


FIGURE 6. The phenology of vegetative bud and shoot development in white spruce. (From Owens *et. al.* 1977.)

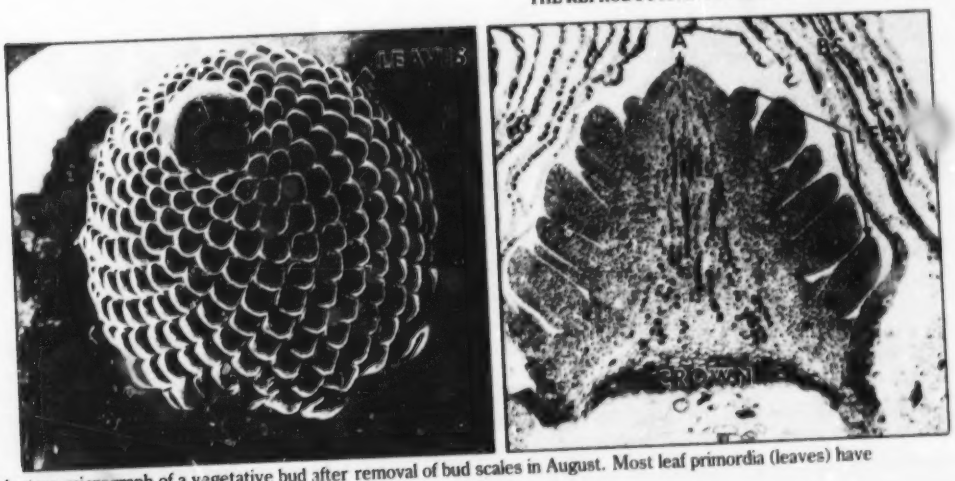


FIGURE 7. Scanning electron micrograph of a vegetative bud after removal of bud scales in August. Most leaf primordia (leaves) have been initiated leaving a small apex (A). (X 30) LEFT

FIGURE 8. Median longitudinal section of a dormant vegetative bud enclosed by bud scales (BS). (X 50) RIGHT

The dormant vegetative bud consists of outer (brown, leathery) bud scales and inner (pale brown, thin) bud scales, which enclose the completely preformed and "telescoped" vegetative shoot. This shoot bears all of the next season's embryonic leaves (leaf primordia) (Figs. 6*A*, 7, 8). When vegetative bud growth begins in the spring, the telescoped shoot axis and leaf primordia elongate, causing the bud to swell (Fig. 6*H*) and then burst (or "flush") through the bud scales (Fig. 6*I*). This is followed by a period of rapid, then slow, shoot elongation (Fig. 6*J*), when shoot and leaf tissues mature and the next years's buds complete development.

One of the first events to occur after dormancy is the initiation of lateral buds. Lateral buds are initiated in the leaf axils of some leaf primordia, that is, just above the juncture of the leaf primordium and the stem (Fig. 15). The apical meristems of the terminal and new lateral buds (Figs. 7, 8) undergo a predictable sequence of developmental events (Figs. 6*B-F*) which correlate with shoot development (Figs. 6*H-J*).

During shoot elongation, the terminal and lateral apical meristems initiate a series of bud scales (Figs. 6*B-C*, 9). At the end of shoot elongation, the apical meristems enlarge rapidly (Fig. 6*D*), and then initiate a series of leaf primordia up the flanks of the apical meristem. The first two-thirds of the leaf primordia are initiated rapidly (Figs. 6*E*, 10), and the remaining one-third of the leaf primordia are initiated more slowly (Fig. 10) until the bud becomes dormant in mid-October (Figs. 6*A*, 8).

Differentiation of Bud Types

After the period of bud-scale initiation, both terminal apical meristems and newly initiated axillary meristems may differentiate into any one of three bud types: vegetative, seed-cone, or pollen-cone. At the time of

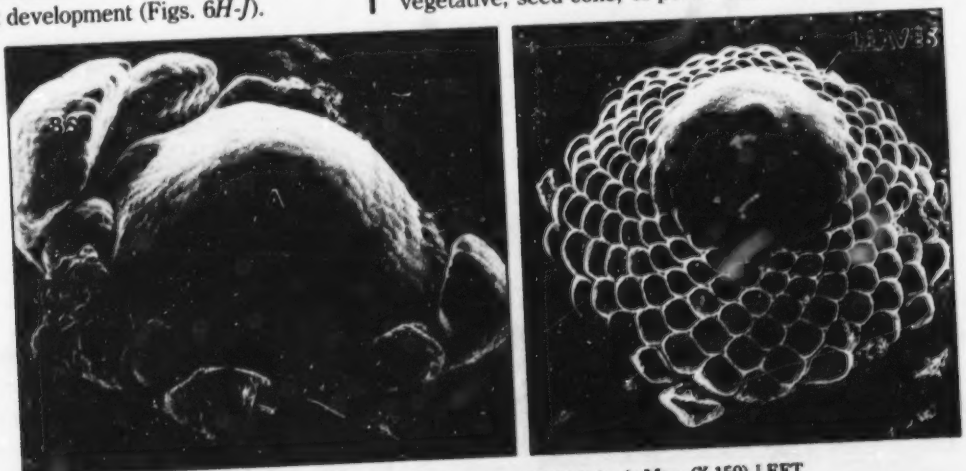


FIGURE 9. Scanning electron micrographs of a vegetative apex during early bud scale (BS) initiation in May. (X 150) LEFT

FIGURE 10. Scanning electron micrograph of a vegetative bud after removal of bud scales during rapid leaf initiation in July. (X 80) RIGHT

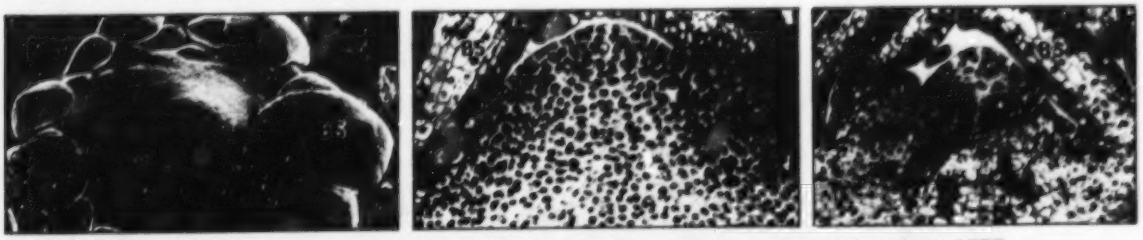


FIGURE 11. Scanning electron micrograph of an undifferentiated apex near the end of bud scale (BS) initiation. (X 100) LEFT

FIGURE 12. Median longitudinal section of a large reproductive apex collected in mid-July. (X 100) CENTRE

FIGURE 13. Median longitudinal section of a small vegetative apex collected in mid-July showing darkly staining phenolic compounds. (X 100) RIGHT

vegetative bud burst, terminal and axillary apical meristems consist only of a small mound of cells enclosed by a few bud scales. Just before shoot elongation is completed, some terminal and axillary apical meristems (Fig. 11) may become more active than others. Their cells divide more frequently and they enlarge rapidly (Fig. 12). These apical meristems develop into either seed-cone or pollen-cone buds. Other apical meristems accumulate abundant phenolic and other unidentified substances (Fig. 13). Cells within these apical meristems divide less frequently, and the meristems develop into vegetative buds (Owens and Molder 1977; Harrison and Owens 1982).

Development of some axillary apical meristems becomes inhibited during bud-scale initiation. Phenolic and unidentified substances accumulate within the buds and cells stop dividing. If this occurs soon after the axillary buds are initiated, the axillary buds degenerate and leave no evidence of their previous existence. These are called aborted buds. Other axillary buds form most of their bud scales before development stops. These buds remain and are called latent buds. Latent buds have not become determined as vegetative or reproductive buds when their growth stops. They consist of a small apical meristem surrounded by many bud scales but with no additional primordia (Fig. 14) (Owens and Molder 1977; Harrison and Owens 1982). Development can often be stimulated in latent buds by the removal of the terminal vegetative bud on the twig. With this inhibition removed, latent buds can usually develop as vegetative buds, forming numerous epicormic shoots — new shoots that develop on older twigs.

FIGURE 14. Median longitudinal section of a small latent bud collected in August showing the apex (A) and bud scales (BS). (X 100)

Pathways of Bud Development

The abundance of cone buds is determined not so much by differences in number of axillary buds initiated (since this varies little from year to year), but more by the pathways along which axillary and terminal buds develop (Fig. 15). In a year when few cone buds develop, many of the axillary buds abort or become latent. In a year when many cone buds develop, few axillary buds abort and many axillary and terminal buds differentiate into pollen-cone or seed-cone buds (Fig. 16). Axillary meristems that likely will not develop are proximal (near the base of the shoot), and are those that would otherwise have developed into pollen-cone buds (Fig. 15).

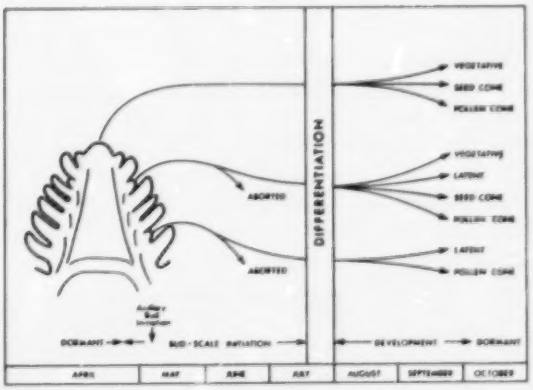


FIGURE 15. Potential pathways of terminal and axillary bud development.

Although both aborted and latent buds can occur along the entire length of the shoot in a year when few cone buds develop, they occur infrequently in the distal (near the tip) regions where vegetative and seed-cone buds normally develop. Thus, it appears, under conditions favourable for reproductive bud development, proximal undetermined axillary meristems develop as pollen-cone buds while the distal undetermined axillary meristems develop as seed-cone buds. Under conditions not favourable for reproductive bud development, most proximal apical

meristems abort or become latent, while most distal apical meristems, rather than becoming latent or aborting, become vegetative buds (Fig. 15).

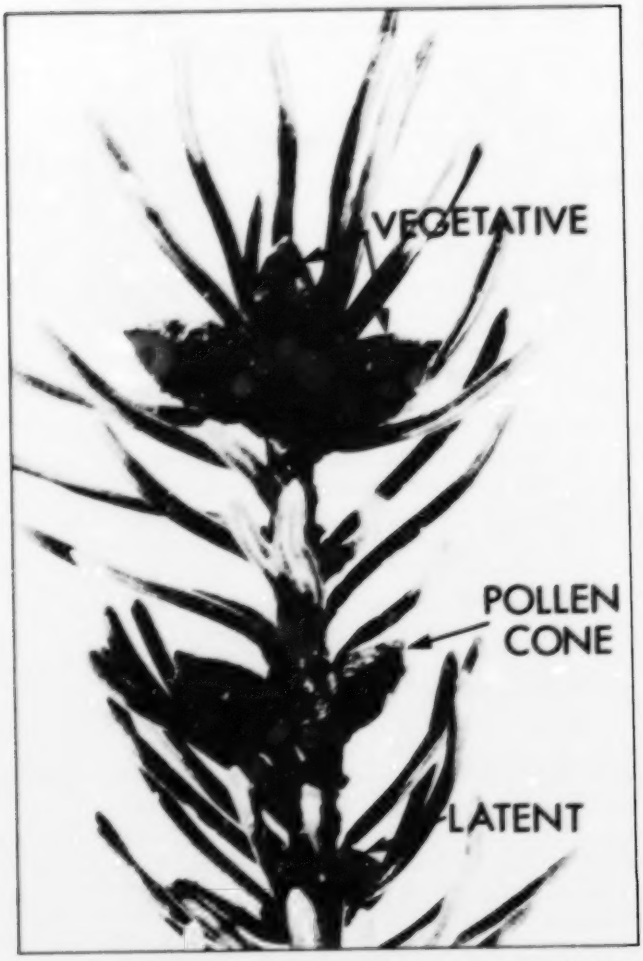


FIGURE 16. Dormant shoot of white spruce showing terminal and distal vegetative buds, and proximal pollen-cone and latent buds. (X 2)

Terminal apical meristems have more limited pathways of development than do axillary apical meristems. When conditions are unfavourable for reproductive bud development, terminal apical meristems remain vegetative. When conditions are favourable for reproductive bud development, terminal apical meristems on vigorous shoots in upper regions of the crown differentiate into seed-cone buds. Terminal apical meristems on less vigorous shoots, or on more proximal shoots in lower regions of the crown, differentiate into pollen-cone buds (Fig. 15) (Owens and Molder 1977; Harrison and Owens 1982).

The position of the cone buds on the shoot will vary somewhat, depending upon the number of cone buds present. In a year when few cone buds differentiate, most occur as terminal cone buds. In a year when many reproductive buds differentiate, the number of terminal cone buds may increase slightly but the number of axillary cone buds increases greatly (Harrison and Owens 1982).

Identification of Buds

Vegetative buds initiate a spiral series of leaf primordia up the flanks of the apex (Fig. 10). By mid-October all leaf primordia are initiated, a crown region begins to develop at the base of the bud (Fig. 8), and the vegetative terminal and lateral buds become dormant. No apical meristems are initiated in the axils of leaves before dormancy. Dormant vegetative buds have a thick layer of 35 to 40 bud scales which enclose the embryonic shoot. The vegetative buds are about 6 mm long (Fig. 17), but the embryonic shoot within the bud is only about 1.5 mm long (Fig. 18). The buds are pointed, light brown and slightly resinous. The terminal vegetative buds often are concealed by the leaves (Fig. 17).

FIGURE 17. Dormant vegetative buds of white spruce. (X 1)

FIGURE 18. Dormant vegetative bud after all bud scales were removed. (X 8)

Seed-cone buds initiate a spiral series of broad bracts and an ovuliferous scale in the axil of all but the most basal and distal bracts. Most ovuliferous scales initiate two lateral ovule primordia on the upper ("adaxial") surface. Seed-cone buds become dormant in mid-October. Dormant seed-cone buds have 30 to 35 bud scales. Seed-cone buds are oblong, pointed, and about 9 mm long (Fig. 19). The embryonic cone within is 2 to 3 mm long (Fig. 20). Bud scales are brown, smooth and slightly resinous (Fig. 19).

Pollen-cone buds initiate a spiral series of broad microsporophylls. Each microsporophyll forms two microsporangia (pollen sacs) on the lower ("abaxial") surface. Each microsporangium contains many pollen mother cells (PMC). Pollen-cone buds become dormant in late September. Dormant pollen-cone buds have 20 to 25 bud scales, are ovate, pointed, and about 7 mm long (Fig. 21). The pollen cone within is about 5 mm long (Fig. 22). Outer scales are brown, smooth and slightly resinous (Fig. 21) (Owens and Molder 1977; Harrison and Owens 1982).

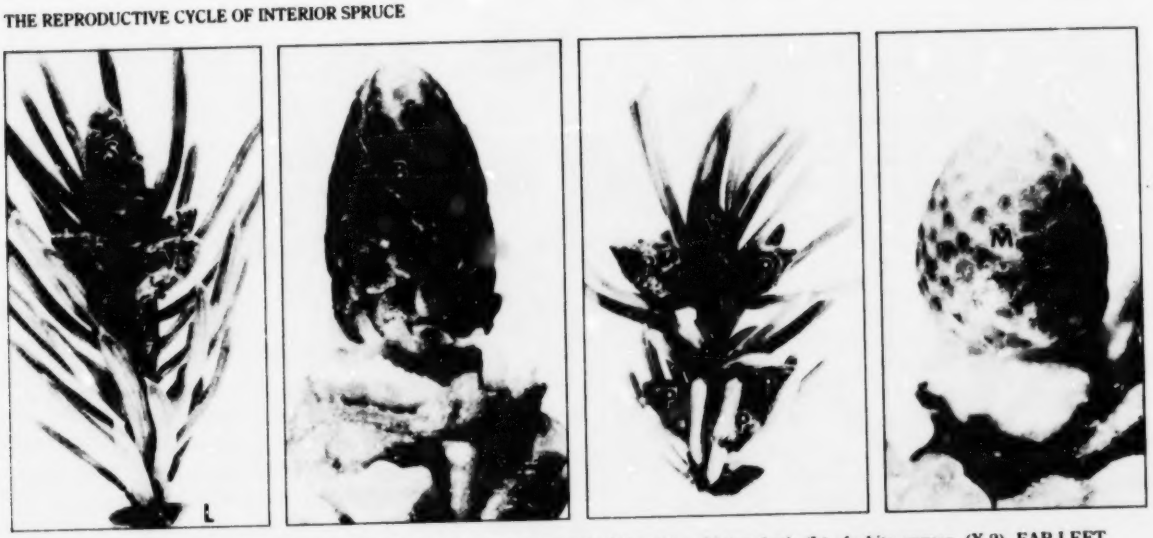


FIGURE 19. Dormant terminal seed-cone bud (S), lateral vegetative buds (V) and basal latent buds (L) of white spruce. (X 2) FAR LEFT

FIGURE 20. Dormant seed cone of white spruce after removal of all bud scales to show the bracts (B). (X 15) LEFT

FIGURE 21. Dormant lateral pollen-cone buds (P) and terminal vegetative bud (V) of white spruce. (X 2) RIGHT

FIGURE 22. Dormant pollen cone of white spruce after removal of all bud scales to show the microsporophylls (M). (X 15) FAR RIGHT

Forecasting Cone Crops

Because the abundance of cone buds varies from year to year it is often useful to estimate the abundance of cones that might be available for pollination and cone collection the following year. The more axillary buds there are that do not abort or become latent during the summer, the more abundant the cone crop is likely to be. This estimate can often be made in August. However, for more accurate estimates of the potential cone crop, branches should be sampled in September from seed-cone and pollen-cone bearing regions of several trees. Buds should be dissected (Figs. 18, 20, 22) or sliced down the centre, then identified and the proportion of vegetative, seed-cone and pollen-cone buds estimated.

FIGURE 23. Branch from a dormant white spruce bearing vegetative (V), seed-cone (S) and pollen-cone (P) buds. (X .3)

Generally, a tree bearing numerous pollen-cone buds at the base of the twig (Figs. 21, 23) will also bear numerous seed-cone buds. (Pollen-cone buds are more easily identified then seed-cone buds.) However, if one tree in a particular location bears many cone buds, this does not ensure that all trees in that area will bear abundant cone buds. In a good year for cone-bud development most trees in an area will likely bear cone buds, but in an average or poor year, only a few trees may bear cone buds. Therefore, an adequate sampling of branches from the upper regions of the crowns of several trees in an area is necessary. It should be emphasized that this method can accurately forecast the lack of a cone crop, though not necessarily an abundant crop. Frost, cone abortion, and insects can seriously reduce a potential cone crop between September of one year, when cone buds can be recognized, and September of the following year when the seeds would be shed (Fig. 5) (Eis and Inkster 1972).

Enhancing Cone-Bud Differentiation

The physiological processes that control the differentiation of axillary or terminal apices into vegetative or reproductive buds in spruce are poorly understood. Environmental factors that appear to favour cone-bud differentiation in spruce (Lindgren *et al.* 1977) and other members of the Pinaceae (Puritch 1972) are high temperatures, abundant sunshine, and

low rainfall preceding and during the time of cone-bud differentiation (Figs. 5, 15). These factors provide environmental stress, reduced vegetative growth, and presumably promote cone-bud differentiation rather than vegetative bud differentiation. Consequently, to remove competition and increase the area of the chosen tree crowns exposed to direct sunlight, thinning the forest is often an effective method of enhancing cone-bud differentiation in a natural stand.

Many specific methods of enhancing cone-bud differentiation have been tried in spruce (Tompsett and Fletcher 1971; Dunberg 1979) and other conifers (Puritch 1972), but have produced variable results according to the species, timing, and methods used. Fertilization promotes flowering in some conifers, but this has not been determined in spruce.[1] Physical stresses, in the form of stem or branch girdling, strangulation and banding, may also enhance cone-bud differentiation in some species. Treatments that limit root growth and presumably water uptake, such as root pruning, root restriction by potting, and transplanting, increase cone production by enhancing the proportion of buds that develop and differentiate into cone buds. However, these treatments, if not properly applied, can result in permanent injury to the tree. All of these treatments must be applied before the time of normal cone-bud differentiation (Figs. 5, 15), but how far in advance of this time is uncertain for spruce.

Many injuries inflicted in nature may also cause stress within the tree, possibly resulting in enhanced cone crops. These can result from frost, fire, logging operations, or disease.

Plant growth regulators (hormones) have been used to induce or enhance flowering in conifers (Puritch 1972). Early attempts used gibberellin A_3 (GA_3) which induced flowering in some species of the Cupressaceae and Taxodiaceae, but not in the Pinaceae. More recently, other gibberellins (GA_4, GA_5, GA_7 and GA_9) have been used to induce flowering in several species of the Pinaceae, including at least three species of spruce: *P. abies*, *P. glauca* and *P. sitchensis*. The best results have been obtained with Norway spruce *(P. abies)* (Dunberg 1979) and Sitka spruce *(P. sitchensis)* (Tompsett and Fletcher 1971).

The best method of treatment has not been determined for interior spruce.[2] Good results for Norway spruce have been obtained when a mixture of gibberellin A_4/A_7 ($GA_{4/7}$) (in 30:70 proportions) has been injected into the xylem or applied as a foliar spray (Dunberg 1979). Injections were made, at a concentration of 400 micrograms of $GA_{4/7}$ in 5 to 10 microlitres of ethanol, by inserting a hypodermic needle into the stem tissue, or attaching a thin plastic tube over the cut end of a twig. In both cases the $GA_{4/7}$ mixture was fed into the stem tissue from a hanging bottle attached to the hypodermic needle or tube. The fluid was taken up with the transpiration stream. It is suggested with this method that frequent checks be made at the point of injection to ensure resin accumulation does not plug the system. Several injection sites may have to be used over several weeks to ensure a constant flow into the tree. Foliar sprays have been applied by spraying trees with 0.2 g of $GA_{4/7}$ per litre of solvent until the spray begins to drip off (Dunberg 1979). The solvent consists of 1.25 g of AROMOX-C cationic detergent in one litre of water, which may promote penetration into the foliage.

Growth-regulator applications generally give best results when used in conjunction with other flower-promoting treatments such as root pruning or water stress. Any cone-enhancing treatment must be applied before and during the time of cone-bud differentiation, which begins about mid-July in white spruce (Owens and Molder 1977) and Engelmann spruce (Harrison and Owens 1982). How long before the time of cone-bud differentiation to commence treatment depends both on the treatment itself and the time it takes for the treatment to reach, and have an effect on, the developing buds.

As in other members of the Pinaceae, treatments that promote flowering in spruce do not appear to increase the total number of axillary bud primordia. Treatments appear to control the pathway along which each terminal or axillary bud primordium will develop (Fig. 15). The potential pathways may be limited by the position of the bud primordium on the shoot, the position of the shoot within the tree, and the age and condition of the tree. For these reasons, and because of variations in individual methods used, highly variable results are often obtained in cone-enhancing experiments.

Pollen-Cone Development

All microsporophylls are initiated before dormancy, and the dormant microsporangia contain many pollen mother cells (PMC) (Figs. 24, 25*B*). No developmental changes occur in pollen cones during dormancy. Pollen-cone buds resume growth and development in mid-April, both in white spruce and Engelmann spruce (Fig. 5). The buds enlarge very slowly for about one month. In the microsporangia, tapetal cells become binucleate and PMCs separate from one another. About mid-May, each PMC undergoes meiosis — a special form of cell division that produces four microspores, each with 12

[1] and [2] Steven Ross, personal communication, 1983, B.C. Ministry of Forests, Research Branch, Victoria, B.C.

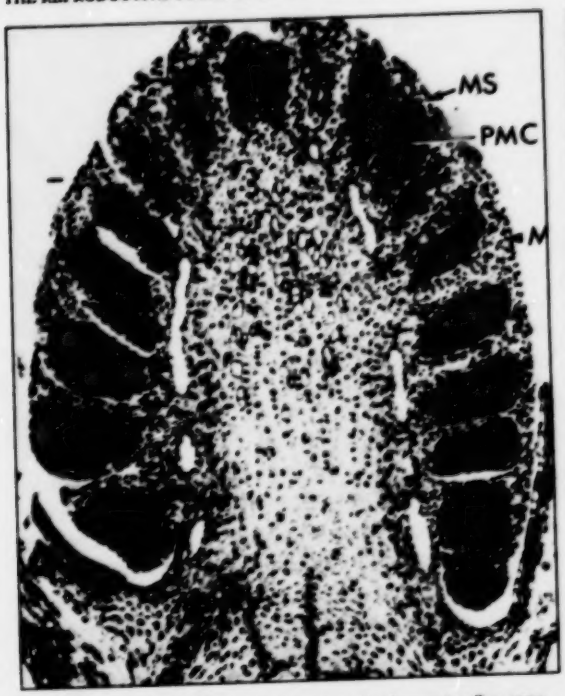


FIGURE 24. Median longitudinal section of a dormant pollen cone showing microsporophylls (M) with microsporangia (MS) containing pollen mother cells (PMC). (X 40)

chromosomes, half ("haploid") the original 24. (Fig. 25*C*). The time of meiosis can usually be detected because the microsporangia, and hence the pollen cones, swell. During the next three to four weeks, each microspore develops into a pollen grain (Figs. 25*D-H*).

Microspores are angular at first, but later round out. A thick wall forms, consisting of two layers: a thin, smooth, inner layer ("intine"); and a thick outer layer ("exine") which has a finely sculptured outer surface. Early in development the exine separates from the intine at two adjacent areas, forming two air-filled wings ("sacci") on the sunken distal surface of the body ("corpus") of the pollen grain (Figs. 25*D*, *E*; 27; 28).

After sacci form, the single haploid microspore divides unequally twice, each time producing a small, lens-shaped prothallial cell (Figs. 25*E*, *F*). The remaining large cell, or "antheridial initial", then divides unequally again, producing a small "generative" cell and a large "tube" cell (Fig. 25*G*) which stores many starch grains. The generative cell divides equally, forming a "stalk" cell adjacent to the prothallial cells, and a "body" cell. This results in a mature five-celled pollen grain which is shed within a few days (Figs. 25*H*, 26-28). The body cell forms two male gametes after pollination.

White and Engelmann spruce pollen grains are microscopically indistinguishable (Figs. 27, 28). The average dimensions of white spruce pollen are as follows: width, including sacci, 92 μ m (84-96 μ m); corpus width 62 μ m (59-65 μ m); corpus length 68 μ m (59-71 μ m); and corpus height 52 μ m (43-74 μ m). The average dimensions of Engelmann spruce pollen are somewhat greater, though the sizes overlap with those of white spruce (Harrison and Owens 1982). Grains have a narrow groove between the sacci, which themselves are large, non-pendulous, and join smoothly to the corpus without conspicuous ridges or projections. The sacci are thin-walled and have an inconspicuous web-like internal reticulum (Fig. 26). Sculpturing is finely granular on the sacci surface and slightly more coarse on that of the corpus (Fig. 27) (Owens and Molder 1979; Singh and Owens 1981; Owens and Simpson 1982).

FIGURE 26. Sectioned mature white spruce pollen. (X 850)

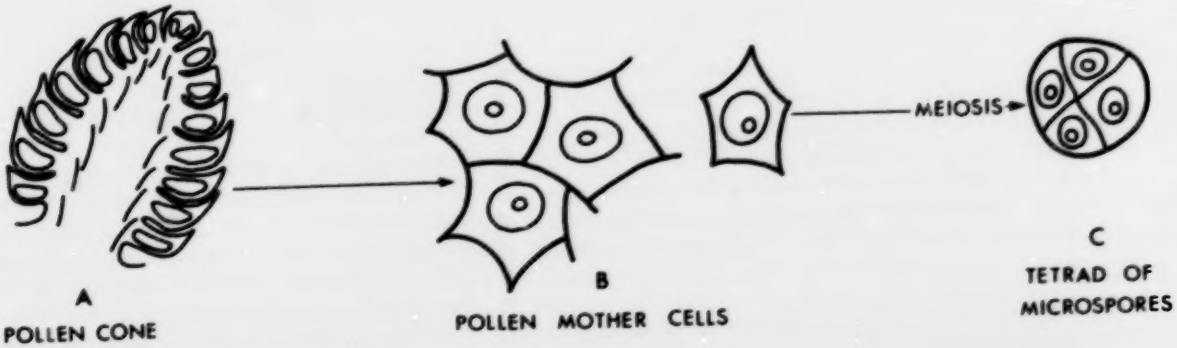


FIGURE 25. Pollen development after winter dormancy.

FIGURE 27. Scanning electron micrograph of white spruce pollen. (X 825)

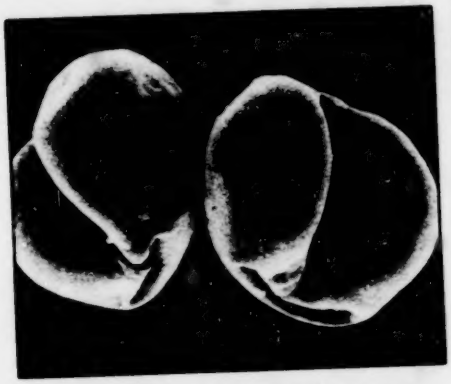


FIGURE 28. Scanning electron micrograph of Engelmann spruce pollen. (X 550)

As the pollen matures, pollen cones elongate and push through their bud scales. The tips of the red pollen cones are often visible beyond the distal bud scales for one to two weeks before pollen is shed. The pollen-cone axis then elongates rapidly and microsporangia split along a predetermined line of dehiscence where the wall is thin. Pollen cones may be horizontal to pendant during pollination. A tree usually sheds the mature, yellow pollen during a one-week period (Fig. 5); and the dried, empty pollen cones may be retained on the tree for several weeks.

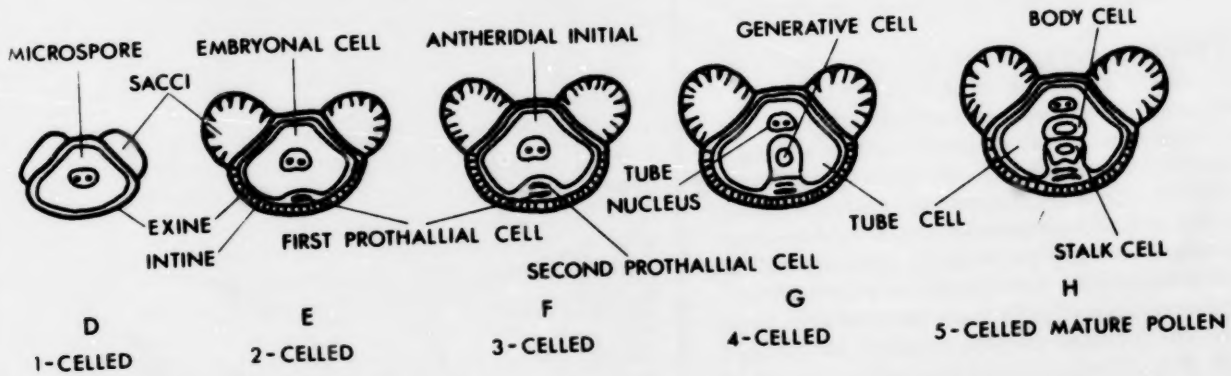
If quantities of good pollen are to be obtained, pollen cones should be collected after they have almost fully emerged from their bud scales and the pollen feels dry to the touch. Pollen cones collected too early, so that the crushed cone yields a yellow, milky liquid, will not open completely and may yield pollen that is immature and inviable. Cones collected after pollen has begun to be shed may yield only small quantities of pollen.

The rate of pollen-cone development after dormancy is greatly affected by temperature, proceeding rapidly during warm weather and slowing during cool or rainy weather. Consequently, much variation in the time of pollen shedding exists between trees, varying by year and area. At low-elevation sites, white spruce pollen cones end dormancy by early April and may shed pollen by the end of May — a period of about two months (Fig. 5) (Owens and Molder 1979). At nearby high-elevation sites, Engelmann spruce pollen cones also end dormancy by mid-April, but, because snow is still deep, development is slower and pollen may not be shed until early July — a period of nearly three months (Singh and Owens 1981). In a seed orchard in the southern interior of British Columbia, both white and Engelmann spruce shed pollen, and seed cones were receptive from mid-April through mid-May[1].

Seed-Cone Development

Seed-cone buds, like pollen-cone buds, resume growth by mid-April in natural stands of white and Engelmann spruce, about 6 and 10 weeks, respectively, before pollination (Owens and Molder

[1]Gyula Kiss, personal communication, 1982. B.C. Ministry of Forests, Research Branch, Victoria.



1979; Singh and Owens 1981). Seed-cone buds form most of their bracts and ovuliferous scales before dormancy (Fig. 29). Some bracts and ovuliferous scales are initiated at the tip of the cone after dormancy, but they produce no seeds. Rarely, in fact, do filled seeds develop near the base or tip of the cone. One reason is that ovuliferous scales at the base and tip of each cone usually display retarded development, and thus do not form fertile ovules by the time of pollination. Another reason is that cone-axis elongation occurs less at the ends of the cone than in the middle, and so restricts pollen entry at the base and tip of the cone.

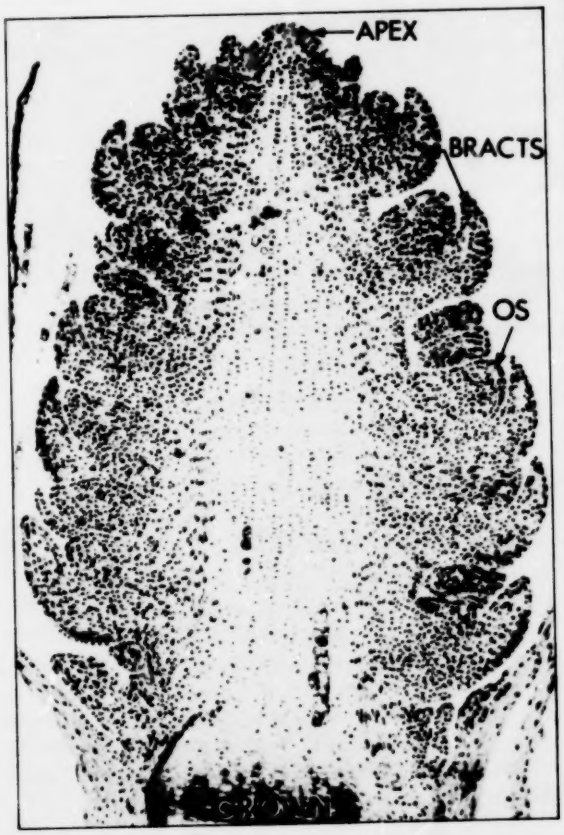


FIGURE 29. Median longitudinal section of a dormant seed cone showing the cone apex, bracts and ovuliferous scales (OS). (X 45)

After dormancy a ring of tissue forms on each ovule at the end adjacent to the cone axis. This tissue elongates to form the integumental tip, which overgrows the megasporangium ("nucellus") (Fig. 30). The integumental tip forms a long, curved, hollow neck that ends in two long micropylar arms. Within the hollow neck the micropylar canal ends at an opening ("micropyle") between the arms (Fig. 31). At pollination the integumental arms extend beyond the ovuliferous scale (Fig. 33) into a space between the cone axis and adjacent ovuliferous scales and bracts (Fig. 34).

FIGURE 30. Scanning electron micrograph of a white spruce ovuliferous scale collected shortly after dormancy showing the two developing ovules (OV) each with a nucellus (N) and elongating integument (IN). (X 40)

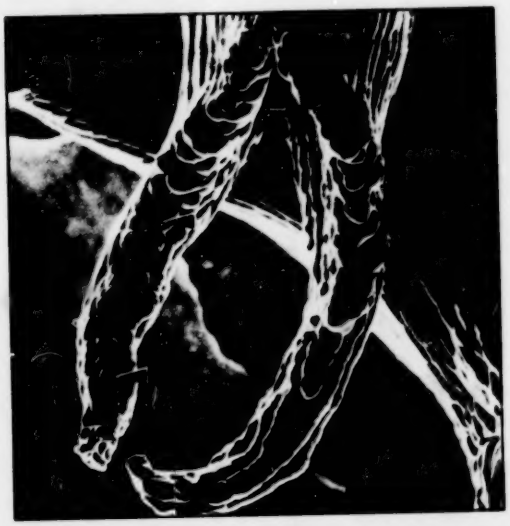


FIGURE 31. Scanning electron micrograph of a white spruce integument tip just before pollination showing the long micropylar arms and the micropyle (M). Minute secretions (arrows) make the arms sticky. (X 110)

Pollination

Pollination is the shedding and transfer of pollen into the ovules of the seed cones. In white spruce, seed cones elongate and begin to emerge from their bud scales in late May (Owens and Molder 1979) (Fig. 5); in Engelmann spruce this occurs in late June (Singh and Owens 1981). Within one to two weeks seed cones emerge fully from their bud scales and are nearly erect on the branches. The cone axis elongates, separating the ovuliferous scales (which bend back), opening the spaces between the ovuliferous scales (Fig. 32), and exposing the small cream-coloured ovules. This allows pollen to sift between the ovuliferous scales and bracts, either adhering to their surfaces or passing directly to the space at the base of the scales where the micropylar arms hang (Fig. 34). Pollen adheres to sticky droplets that are exuded from

FIGURE 32. White spruce seed cone at pollination. (X 3)

the cells covering the inner surface of the micropylar arms (Fig. 31).

From the nucellar tip a fluid is then discharged, forming a large pollination drop between the micropylar arms. This drop picks up pollen adhering to the micropylar arms, or pollen may land directly on the drop. Either way, the pollination drop is retracted into the micropylar canal, carrying with it any trapped pollen. As the pollination drop dries, pollen is drawn into the pollen chamber, a depression in the tip of the nucellus. Some pollen adheres to the sides of the micropylar canal as the pollination drop is drawn down the canal. The micropylar arms are usually widely spread when the pollination drop is exuded (Figs. 33, 34), but the arms wither and collapse after the drop is withdrawn.

FIGURE 33. Adaxial (upper) surface of a white spruce ovuliferous scale showing two ovules (OV) with their micropylar arms (MA). (X 40)

FIGURE 34. Abaxial (lower) surface of a white spruce bract and ovuliferous scale (OS) showing the micropylar arms (MA) extending into the chamber (CH) between ovuliferous scales (X 25)

Only a few ovules exude a pollination drop at any one time. It is not known how many times an ovule can discharge a drop or, once pollen has been taken into the ovule, whether another drop is discharged. Within approximately one week after pollination drops are withdrawn, the ovuliferous scales thicken and close, sealing the cone against further effective pollination.

The optimal time for pollination is reached when the pollination drops have formed. Determining this, however, requires cone dissection, and the pollination drop is then often difficult to see. The time can be approximated since it occurs soon after the seed-cone axis elongates and exposes the bracts and ovules. Before elongation, pollen adheres only to the cone surface and outer edge of the ovuliferous scales. After the receptive period the closed ovuliferous scales prevent pollen from reaching the ovules. The most receptive time lasts only four to six days for a cone, but is longer in a tree because of the variation in rate of seed-cone development. Cool or wet weather at pollination may prolong the receptive period, whereas, warm, dry weather may shorten it.

Ovule Development

In dormant seed-cone buds of both the white and Engelmann spruce species, each rudimentary ovule contains a single large megaspore mother cell (MMC) which is surrounded by spongy tissue that in turn is enclosed within the megasporangium (nucellus) (Figs. 38*A*, *B*). Soon after dormancy ends, the megaspore mother cell enlarges (Fig. 35) and, within three to four weeks, divides by meiosis to form four megaspores (Figs. 36, 38*C*), each with half the original 24 chromosomes. The three outer megaspores

FIGURES 35-37. Median longitudinal sections of ovules.

FIGURE 35. Large megaspore mother cell (MMC). (X 700) LEFT

FIGURE 36. Four haploid megaspores. The outer three are degenerating megaspores (DM) and the inner functional megaspore (FM) is enlarging. (X 300) CENTRE

FIGURE 37. Early free nuclear female gametophyte (FG) (X 300) RIGHT

degenerate (Figs. 36, 38*C*) and the inner, large, functional megaspore develops into the female gametophyte. Development occurs in the same manner and at about the same rate in both species.

The functional megaspore enlarges, becomes filled with many vacuoles, and begins a series of nuclear divisions that are not followed by cell divisions. After many of these free nuclear divisions (Fig. 37), an irregular sac-like female gametophyte forms, consisting of a thin peripheral layer of cytoplasm containing many free nuclei and a large central vacuole (Fig. 38*E*). The female gametophyte is bounded by the megaspore cell wall, which later thickens (Figs. 38*F*, *G*) and may become sculptured much like the wall of the pollen grain. Outside the megaspore wall is a spongy tapetum, which degenerates during female gametophyte development (Figs. 38*E*, *F*), adding to the thickness and sculpturing on the surface of the megaspore wall.

The female gametophyte enlarges for two to three weeks, and then cell walls form rapidly, dividing the female gametophyte into many large uninucleate cells (Fig. 38*F*). Most of these cells divide and form many small cells. At the micropylar end of the female gametophyte, several cells do not divide but elongate and function as archegonial initials (Figs. 38*F*, 39). Around the large archegonial initials several small cells remain. These cells form a single layer of archegonial jacket cells, enclosing each archegonium except at the micropylar end. Each archegonial initial enlarges, becomes vacuolate, and then divides unequally, producing a small primary neck cell at the micropylar end, and a large central cell (Figs. 38*G*, 40). Each primary neck cell divides to form one layer of neck

FIGURE 39. Longitudinal section of a cellular female gametophyte showing an archegonial initial (AI). (X 325)

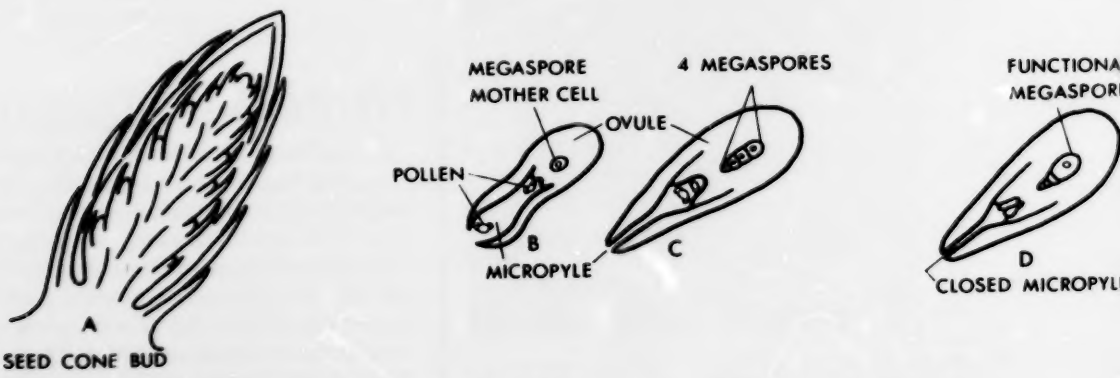


FIGURE 38. Female gametophyte development in white and Engelmann spruce.

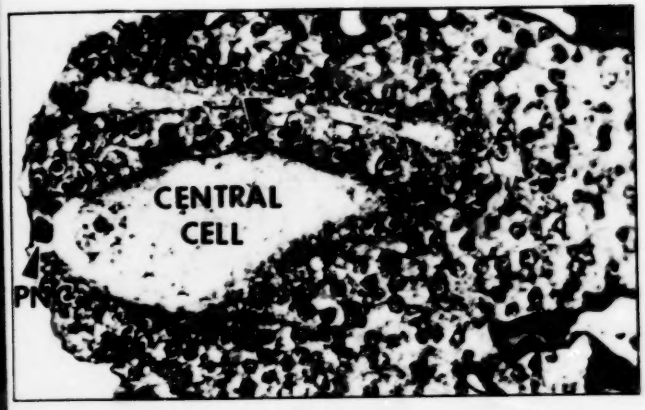


FIGURE 40. Longitudinal section of a female gametophyte showing the large central cell surrounded by the archegonial jacket (AJ) and the small primary neck cell (PNC). (X 180)

cells (Fig. 38*H*). Many large vacuoles form in the central cell, giving it a frothy appearance (Fig. 38*G*). The vacuoles become filled with large and small inclusions often referred to as "proteid bodies" (Fig. 41). During this process, the central cell divides unequally to form a small ventral canal cell, adjacent to the neck cells, and a large egg cell. When the egg cell nucleus migrates to the centre of the egg cytoplasm, the female gametophyte is mature and ready for fertilization (Figs. 39*H*, 41). A single female gametophyte of either spruce species may have one to four archegonia, but three is most common.

The female gametophyte is mature in white spruce in late June, and in Engelmann spruce in late July or early August. This is approximately one month after pollination in each species (Fig. 5). During female gametophyte development the ovules and seed cones enlarge to their final size. At this stage, seed cones are pendant and green, but not woody. During later stages of female gametophyte development, the seed coat differentiates from the integument and the ovule becomes very hard (Owens and Molder 1979; Singh and Owens 1981).

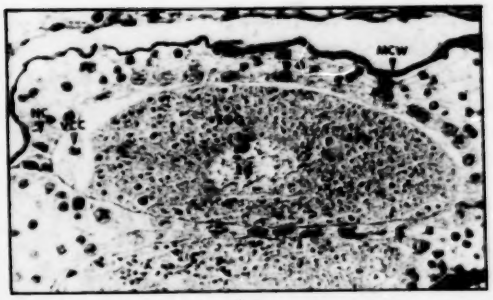
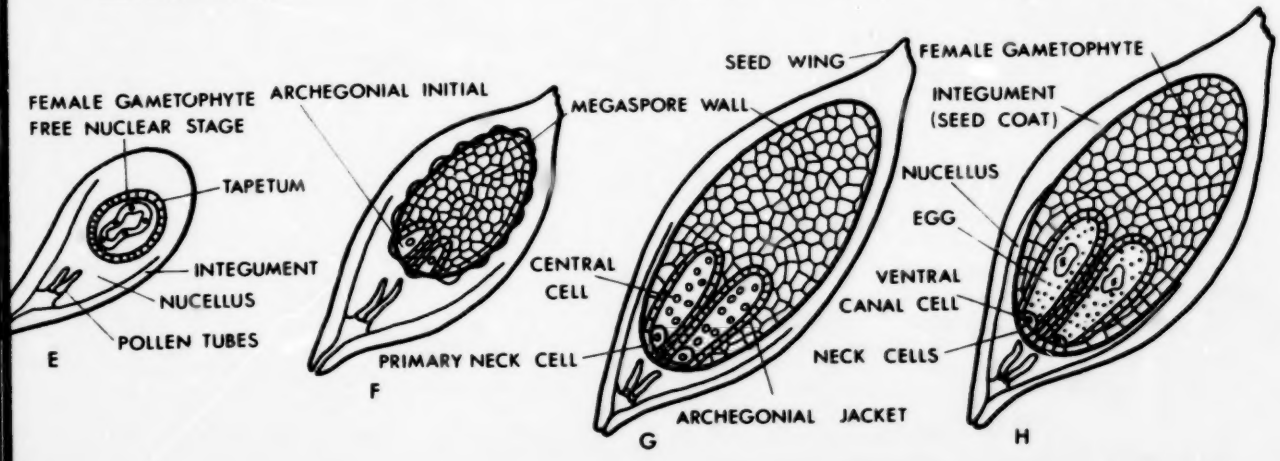


FIGURE 41. Median longitudinal section of part of a mature female gametophyte showing an archegonium. NC, neck cells; VC, ventral canal cell; AJ, archegonial jacket; EN, egg nucleus; PB, proteid bodies; MCW, megaspore cell wall. (X 270)

Fertilization

Pollen grains germinate approximately two weeks after pollination. Pollen tubes grow through the nucellus and reach the neck cells just before the female gametophyte is mature. The tip of a pollen tube splays out over the depression above the neck cells, and a narrow extension of the pollen tube grows between the neck cells and through the ventral canal cell. The contents of the pollen tube are then released into the egg cell (Figs. 42, 46*A*). A receptive vacuole

FIGURE 42. Section through an archegonium at fertilization showing the pollen tube (P), neck cells (NC), ventral canal cell (VCC), two male gametes (G) and the egg nucleus (EN). (X 270)



usually results from the discharge of the contents of the pollen tube into the egg cytoplasm.

Although several pollen grains may germinate on each nucellus, normally no more than one pollen tube reaches each archegonium. During pollen-tube growth, the body cell of the pollen grain divides to form two unequally sized male gametes. The male gametes (Fig. 42) lack any visible means of movement, but, despite this, the larger male gamete migrates through the egg cytoplasm and fuses with the egg nucleus in the centre of the egg cell (Fig. 46*A*), thus completing fertilization. The smaller male gametes and other contents from the pollen tube degenerate. Fertilization in white spruce occurs in late June or early July (Fig. 5), and in Engelmann spruce in late July or early August. In both species this is approximately one month after pollination.

Embryo Development

As in other conifers, embryo development in spruce is separated into two phases: a short proembryo phase, which occurs within the archegonium; and an embryo phase which occurs after the proembryo elongates into the female gametophytic tissue (Singh 1978). The latter phase is commonly separated into several stages. Embryo development occurs entirely within the female gametophytic tissue, which serves as the stored food for the developing embryo.

FIGURE 43. Section of an archegonium showing three of the four free nuclei (arrows) of the proembryo. (X 120)

Proembryo development begins when the fertilized egg nucleus divides into two (Fig. 46*A*), then four, free nuclei contained within a dense region of cytoplasm ("neocytoplasm") in the centre of the egg cell. The neocytoplasm and the four nuclei migrate to the end of the egg cell opposite the neck cells (Fig. 43). The nuclei become oriented into a single tier (Fig. 46*B*), and each nucleus divides. Cell walls form between the eight nuclei to create two tiers of four cells each (Figs. 44, 46*C*). Each cell divides again, forming a 16-celled proembryo consisting of four tiers of four cells each (Figs. 45, 46*D*). The proximal "open

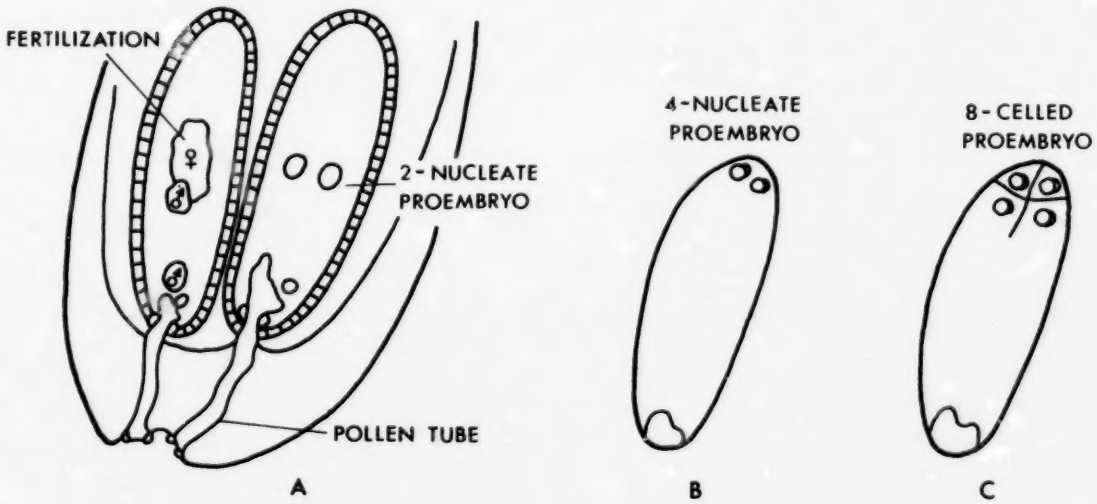


FIGURE 46 *A-H*. Fertilization and embryo development in spruce.

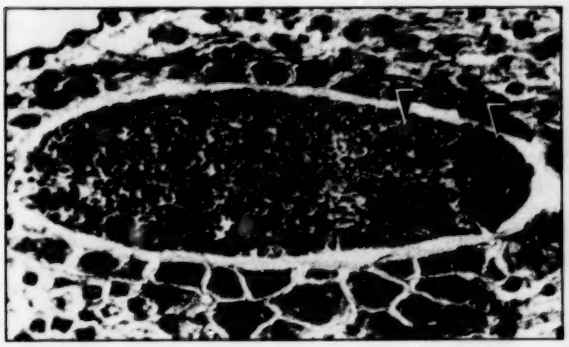
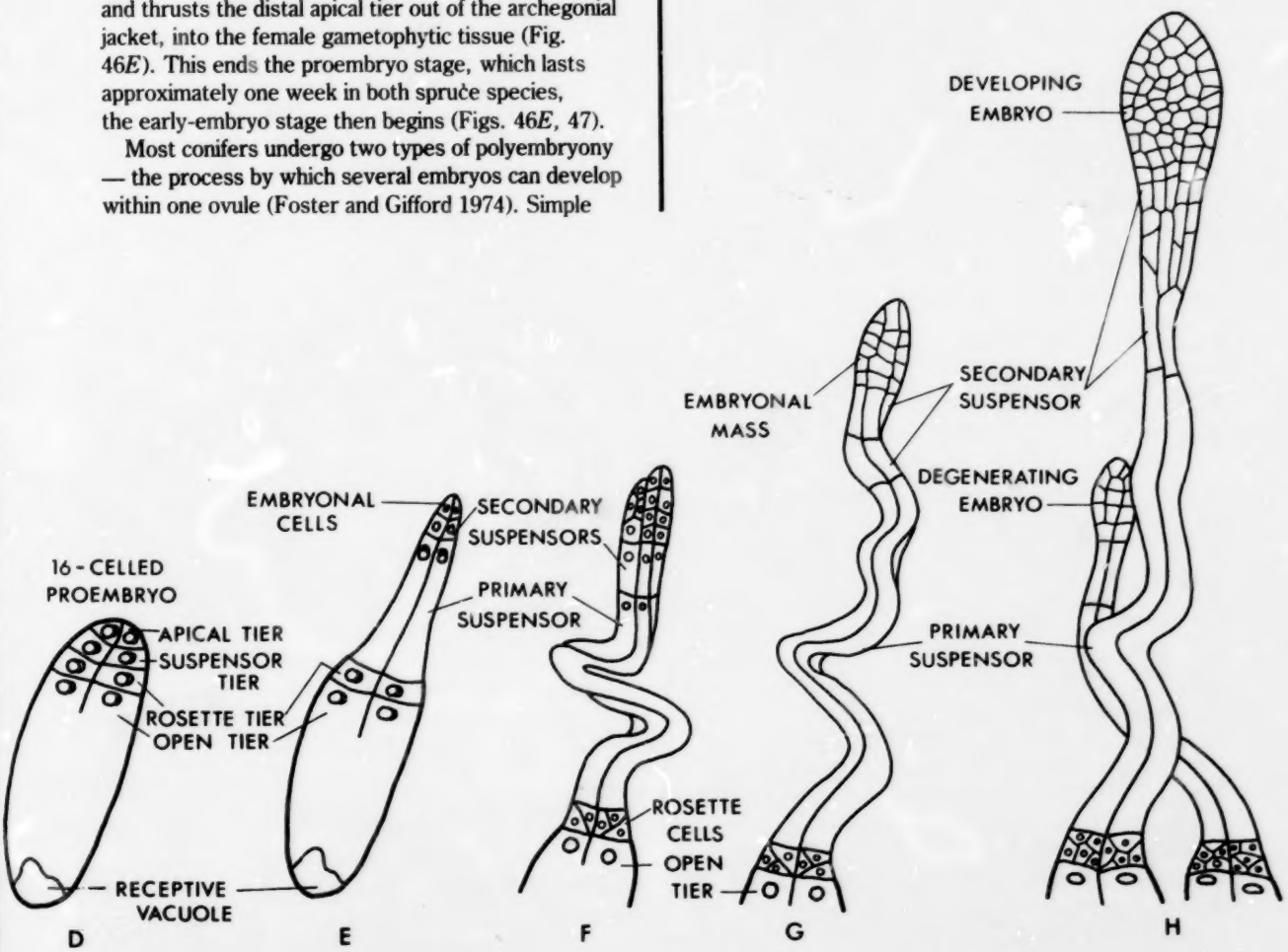


FIGURE 44. Section of an eight-celled proembryo in the archegonium. Each tier consists of four cells. (X 210)

FIGURE 45. Sectio[illegible]rt of a sixteen-celled proembryo showing the distal apica[illegible]ier (A), suspensor tier (S), rosette tier (R) and open tier (O). Only two of the four cells are visible in each tier. (X 220).

tier" remains receptive to the egg cytoplasm and apparently functions to absorb nutrients stored in the egg cytoplasm. The adjacent "rosette tier" has no known function, but may divide and form small clumps of cells — often mistakenly called "rosette embryos". The third tier of cells, the "suspensor tier", elongates and thrusts the distal apical tier out of the archegonial jacket, into the female gametophytic tissue (Fig. 46*E*). This ends the proembryo stage, which lasts approximately one week in both spruce species, the early-embryo stage then begins (Figs. 46*E*, 47).

Most conifers undergo two types of polyembryony — the process by which several embryos can develop within one ovule (Foster and Gifford 1974). Simple polyembryony occurs when more than one egg is fertilized within an ovule. White and Engelmann



spruce usually have about three eggs per ovule and commonly more than one egg is fertilized. Each resulting proembryo could develop into a mature embryo (Figs. 46*H*, 47). In simple polyembryony, each proembryo is a result of fertilization by gametes from separate pollen grains and, therefore, the proembryos are genetically different. One proembryo is usually more vigorous and continues development while the others degenerate (Fig. 46*H*).

A second type of polyembryony, "cleavage" polyembryony, occurs when the suspensor tier elongates. Cleavage refers to the separation of the apical cells into four files of cells, each of which can develop into a separate, but genetically identical, embryo (Foster and Gifford 1974). This type of polyembryony is not known to occur in spruce. However, in white and Engelmann spruce, not all four cells of the apical tier contribute equally to the embryo. One or more cells may divide more frequently, overgrow the others, and contribute more to embryo development (Singh 1978).

Cells of the apical tier divide, forming terminal embryonal cells and subterminal secondary suspensors (Fig. 46*E*). This forces the terminal embryonal cells still deeper into the female gametophyte. The embryonal cells divide, creating an embryonal mass (Figs. 46*F*, *G*). The basal cells of the embryonal mass continue to divide and elongate, contributing to the thick secondary suspensor. Distal cells of the embryonal mass divide to form a club-shaped embryo (Figs. 46*H*, 48).

The club-shaped early embryo that survives the simple polyembryonic selection process enlarges rapidly, filling the corrosion cavity that forms in the female gametophyte (Fig. 48). Specific meristematic regions appear, marking the beginning of the late embryo stage. In white spruce this begins in mid-July, two months after pollination (Owens and Molder 1979), and in Engelmann spruce in early August, six weeks after pollination (Singh and Owens 1981). A core of slightly elongated cells forms the embryonic stele. The root apical meristem forms near the centre of the embryo and the cotyledon primordia arise in a ring around the distal end of the embryo. A tiny stem apical meristem remains between the cotyledons (Fig. 49). The embryo then goes through a one-month period of growth and development before cells stop dividing and the embryo is mature. During this time the hypocotyl (embryonic stem) and cotyledons elongate, and provascular tissue appears. The stem apical meristem remains small and inactive, while the root apical meristem forms a massive root cap (Fig. 49).

As the embryo extends into the female gametophyte, stored food is dissolved and a region of clear cells is left around the embryonal mass (Figs. 47, 48). These female gametophytic cells degenerate, forming a corrosion cavity in which the embryo develops (Figs. 47, 48). The remaining female gametophytic cells accumulate storage products in the form of starch and lipo-protein, which are used during seed germination (Figs. 48, 49).

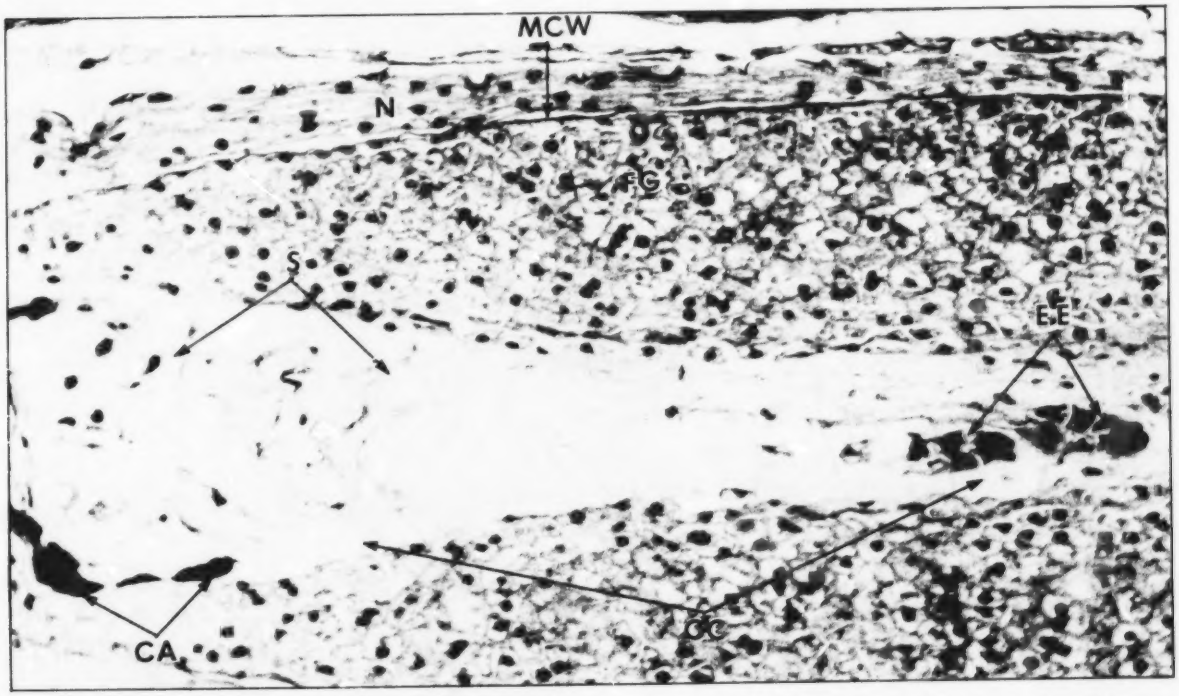


FIGURE 47. Longitudinal section of a developing seed showing two early embryos (EE) and the coiled suspensor (S) in the corrosion cavity (CC) of the female gametophyte (FG). (N), nucellus; (MCW), megaspore cell wall; (CA), collapsed archegonia. (X 105)

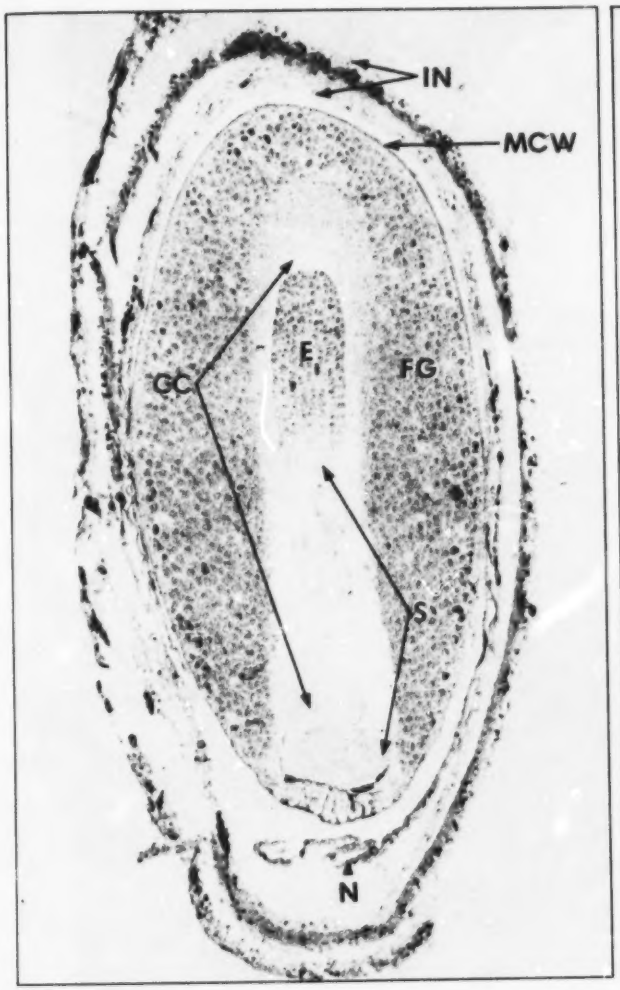


FIGURE 48. Longitudinal section of a developing seed containing a club-shaped embryo (E) collected in mid-July. (S), suspensor; (CC), corrosion cavity; (FG), female gametophyte; (N), nucellus; (IN), integument; (MCW) megaspore cell wall. (X 40)

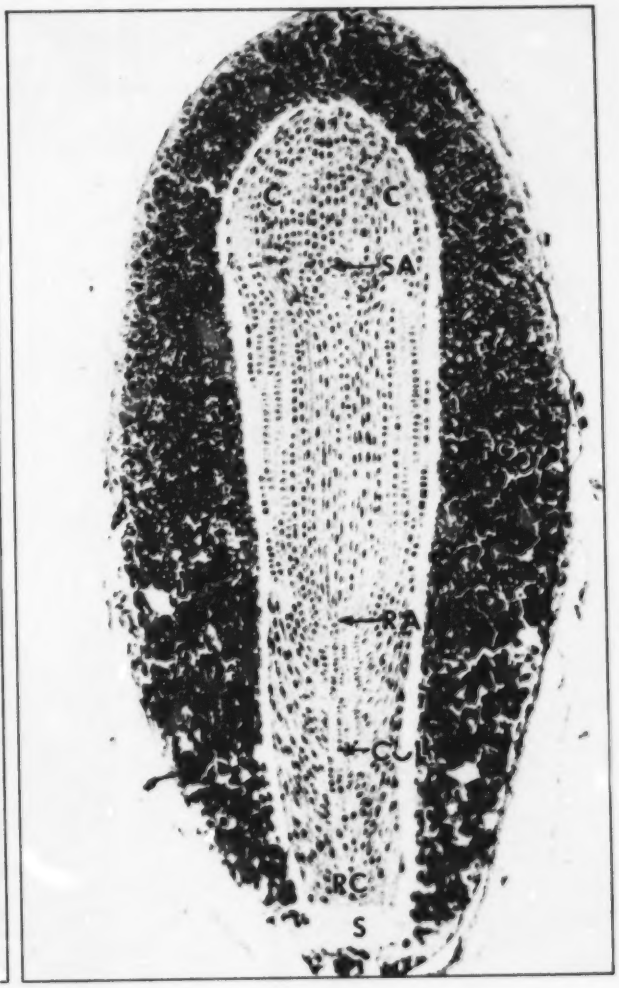


FIGURE 49. Longitudinal section of a mature seed. (FG), female gametophyte filled with dark storage products; (S), suspensor; (C), cotyledons; (SA), stem apical meristem; (RA), root apex; (COL), column; (RC), root cap. (X 40)

Seed Development

The seed coat ("testa") begins to differentiate from the integument before fertilization. The integument forms three distinct layers characteristic of coniferous seed: (1) the thin, dark outer layer, which is fused with the seed wing; (2) the thick, hard middle layer; and, (3) the thin inner layer, which lies adjacent to the nucellus (Foster and Gifford 1974; Singh 1978).

A seed wing develops from the ovuliferous scale and is attached to the end of the seed opposite the micropyle (Fig. 51). At pollination the seed wing begins to differentiate from surface cells of the ovuliferous scale, and at fertilization a distinct seed wing, two to three cells thick, is formed. A separation layer develops beneath the ovule and seed wing during early embryo development, and complete separation of seed and seed wing from the ovuliferous scale occurs before the embryo is mature (Owens and Molder 1979; Singh and Owens 1981).

In the mature seed the embryo is loosely packed within the rather firm, white nutritive female gametophytic tissue, often called "endosperm" (Figs. 49, 50). A thin megaspore wall encloses the female gametophyte. The cells of the nucellus become compressed during embryo development and degenerate before the seed is mature. The seed of white spruce at lower elevations is mature in late August (Owens and Molder 1979) and shed in a five-week period from late August through September, whereas Englemann spruce may shed seed into October. Approximately 10 percent of the seed may be retained in the cones and shed during the winter or the following spring (Fowells (compiler) 1965).

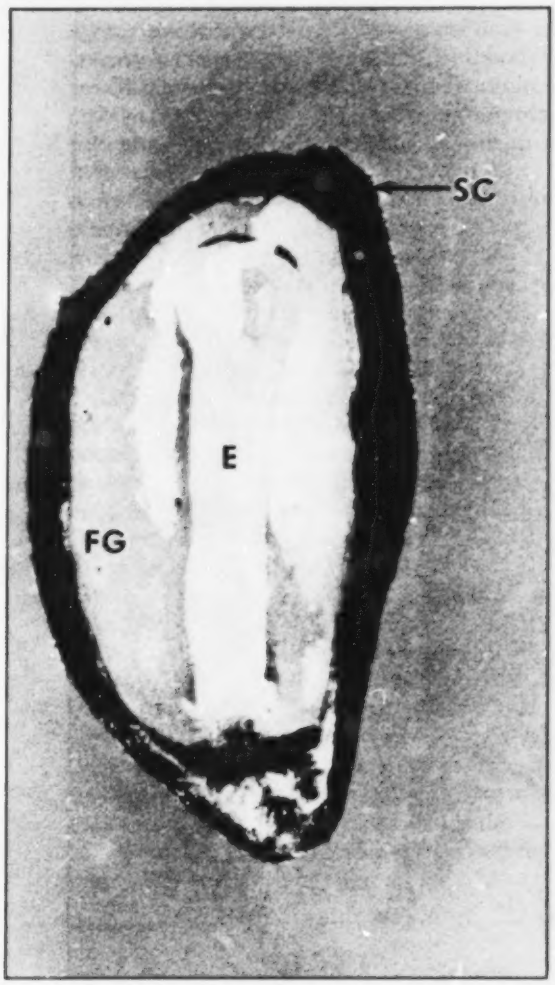


FIGURE 50. White spruce seed dissected to show the seed coat (SC), female gametophyte (FG) and mature embryo (E). (X 30)

FIGURE 51. White spruce seed and seed wing. On the left, is the upper surface of an empty seed. On the right is the lower surface of a filled seed. (X 10)

Both spruce species are relatively good cone producers at lower elevations, but at higher elevations the number of cones produced may decrease. As well, seed cones from higher-elevation trees are often smaller and contain fewer seeds than cones of lower-elevation trees of the same species. Consequently, it is difficult to give an average number of seeds per cone. The number of filled seed per cone in white spruce has been reported at between 59 and 109, with an average of 80 seeds per cone (Fowells (compiler) 1965). These estimates may be high, however, with averages of 30 filled seeds per cone being more common[1]. Information for Engelmann spruce is more limited, although approximately 40 seeds per cone have been obtained from Engelmann spruce growing in southern British Columbia[1].

[1]Gyula Kiss, personal communication, 1982, B.C. Ministry of Forests, Research Branch, Victoria.

Ovules at the base and tip of the cone either do not develop at all, or develop more slowly than ovules from the central portion. Those ovules whose development is arrested or retarded may not be pollinated or fertilized, and they may develop female gametophytic tissue that will later abort when an embryo fails to develop. These commonly form small, flat, empty seeds. As well, seeds from the fertile central portion of the cone may be empty because they were not pollinated or fertilized, or because the embryo aborted. Since pollen is not needed for ovule development, these unpollinated seeds develop a normal female gametophyte and a rounded ovule, but the former degenerates during the period of embryo development, leaving a normal-appearing, but empty seed. Other ovules in the fertile portion of the cone may abort soon after pollination and form small, flat, empty seeds as in the non-fertile portions of the cone. The most common causes for empty or otherwise inviable seed in both spruce species are a lack of

pollination, insect damage and embryo abortion (Owens and Molder 1979; Singh and Owens 1981).

Seeds are small in both spruce species. White spruce seeds (Figs. 51, 52) are the smaller of the two, with approximately 513 000 seeds/kg. Engelmann spruce seeds number approximately 485 000/kg of cleaned seeds (Fowells (compiler) 1965; Dobbs *et al.* 1976; Singh 1978). The seed wings are relatively large for the seed size (Fig. 51), and consequently seed dispersal in open areas from mature trees is commonly 100 m, and can extend to over 300 m

FIGURE 52. Dewinged seed of white spruce. (X 10)

(Dobbs 1976). Many seeds, because of their small size, are missed by rodents.

Generally, white spruce and Engelmann spruce at lower elevations are moderate to good seed producers, whereas higher-elevation trees are relatively poor seed producers at most locations. Seed-production potential can be decreased by the unsettled weather often encountered at higher elevations at the time of pollination, especially in Engelmann spruce zones. Several cone insects decrease seed production in both species, especially in years of low or moderate cone production (Hedlin *et al.* 1980).

In the two spruce species, seeds that are shed in the fall or winter will normally germinate in June or July, as soon as temperatures become favourable for the particular site. Sometimes the seeds may not germinate until the second summer. Natural seed-beds must be moist because first-year seedlings have a shallow, slow-growing root system. Both spruce species are relatively shade tolerant, but do not survive well when growing with the more shade-tolerant conifers such as *Abies* species, or fast-growing broad leafed perennials. Engelmann spruce seedlings seem to establish themselves under more varied and severe conditions than do white spruce seedlings (Fowells (compiler) 1965; Dobbs 1972).

Cone Collection, Seed Extraction, Storage, and Germination

The proper time of cone collection is important and will vary by site and by year. To determine the correct time, it is recommended that a fresh cone from six or more trees in an area be sampled periodically, beginning in August. The average moisture content for three samples of two cones each, or average specific gravity of six individual cones, will provide an accurate measure of seed ripeness. Cones should be collected when the moisture content falls to 48 percent of wet weight, or specific gravity reaches about 0.74. Alternatively, in the field, a test of 10 fresh cones may be made in a jar of turpentine or kerosene. Collections should begin when an average of nine cones float in turpentine, or eight in kerosene (Cram and Worden 1957). Earlier collections may contain cones in which seed is not mature or cones are too wet to dry properly.

Once collected, cones can be stored in sacks in a dry area. Some cones may open during storage. Often immature or very wet cones become moldy during storage and mold inside the cone can cause seeds to adhere to the ovuliferous scales, preventing seed extraction.

Immature cones and seeds can be artifically ripened during storage. White spruce cones collected as early as 1 August and kept in cold-air (5°C) storage with high humidity (75-95%) were found to produce seed with high germination capacity (Winston and Haddon 1981). It appears that once embryo enlargement occurs, artificial ripening of seeds is possible because, during late embryo development, the seeds separate from the ovuliferous scales but are retained within the cones. From that time onward, the seeds rely on stored nutrients in the ovules, rather than on nutrients obtained directly from the cone or the parent tree.

The temperature currently used for open spruce-cone extraction is approximately 42°C for 13 hours. Cleaning of seeds and removal of seed wings (Figs. 51, 52) must be done carefully so that the thin seed coat is not damaged. Any damage to the seed coat may greatly reduce the storage life and viability of the seed. White and Engelmann spruce seeds having a moisture content of six to nine percent may be stored at -19°C in air-tight bags for several years without a significant decrease in viability.[1]

In the past, no pre-sowing treatment of white spruce seeds was considered necessary. For Engelmann spruce, however, stratification at about

[1]Gyula Kiss, personal communication, 1982, B.C. Ministry of Forests, Research Division, Victoria.

2°C for 21 to 24 days was recommended (Safford 1974). It has since been shown that the need for pre-sowing treatment of interior spruce seeds depends upon the seed source (Wang 1974). White spruce seeds from central British Columbia germinate best after two weeks' stratification, whereas Engelmann spruce seeds from southern British Columbia germinate well without any stratification.[1] The British Columbia Ministry of Forests Seed Centre stratifies the seeds of both spruce species for four weeks at 1-3°C before sowing.

The Seedling

Seedlings of both species have several cotyledons. After germination the shoot apical meristem passes through a phase of free growth during which primary leaves are initiated. These leaves elongate immediately (Fig. 53). During this first year, induced

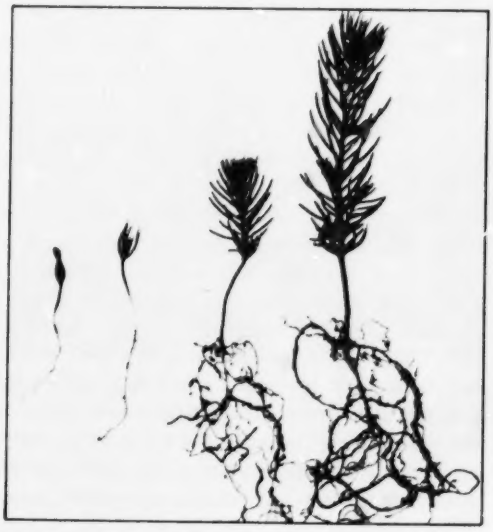


FIGURE 53. Stages of white spruce seedling development during the first growing season. (X .6)

photoperiods, or the natural short photoperiods of late summer, will cause the apical meristem to initiate a series of bud scales, followed by a series of leaf primordia which normally do not elongate before dormancy (Pollard 1974). The bud scales and the enclosed leaf primordia make up the dormant vegetative bud, characteristic of older trees. Vegetative buds can occur in the axils of some of the primary leaves. These buds contain leaf primordia which may elongate during the first year of seedling growth, or they may form small, dormant, axillary vegetative buds that flush after dormancy (Fig. 53). Normally, in the second and subsequent years, terminal and axillary vegetative buds elongate and follow the same development sequence of bud scale initiation-leaf initiation-dormancy, as was described for mature trees (Fig. 6).

[1]Gyula Kiss, personal communication, 1982, B.C. Ministry of Forests, Research Division, Victoria.

Summary

The reproductive cycles of white and Engelmann spruce are essentially the same, though considerable variation may occur in the phenology of reproductive development at different latitudes or different elevations. Elevational differences are clinal, with development usually beginning later and finishing earlier as elevation increases. The reproductive cycles of both species extend over approximately 14 to 15 months, which is similar to many other conifers where cone initiation occurs the first year, and pollination, fertilization, and ovule and seed development occur the second year. During this time, many environmental and physiological factors, not fully understood, may affect development of cones and viable seeds.

One of the most common causes for the absence of a cone crop is failure to initiate many cone buds. Like numerous other conifers, the occurrence of cone crops is very cyclic, perhaps only every two to six years, and even less frequently at the higher elevations where Engelmann spruce commonly grows. A second weak link in the reproductive cycle is pollination, which again may be especially poor at high-elevation sites. Pollinated ovules often do not develop into filled seed because of early embryo abortion. Under seed-orchard conditions, many factors which adversely affect viable seed production may be overcome, or at least minimized, and a high yield of high-quality seed might be obtained. Understanding the complete reproductive cycles of white and Engelmann spruce is a first, essential step in the promotion and control of cone and seed production for reforestation of these two commercially important species.

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